RATTUS GREYI GRAY AND ITS DERIVATIVES

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3 Plates and Text Fig. 1

CONTENTS

1. INTRODUCTION

The original form of this distinctive Australian rat was described by J. E. Gray (1841) from two cotypes sent to London from South Australia. Captain G. Grey, who is traditionally credited with being their collector, visited South Australia unofficially in 1840, before his assumption of the governorship of the province in the following year, and it has been generally accepted that the locality "vicinity of Adelaide" quoted in the appendix on mammals in his Journal, is to be accepted literally in localizing the type. While the circumstances of this early Colonial time might be thought to render this probable enough it cannot be regarded as definitely established and some evidence to the contrary is later presented (*infra*).

No further systematic work was done on the species for more than 80 years, during which time several "records" of it were later shown (or have come to be regarded) as erroneous and based on misidentifications (Collett, 1887; Ogilby, 1892; Waite, 1896). It is somewhat remarkable that Gould who also travelled widely in the State did not recognise the distinctness of "*Mus greyi*" of Gray, but relegated that name to the synonymy of *Mus gouldi* Waterhouse (now referred to *Thetomys*); and later (1858) in describing *R. assimilis* from New South Wales, which is so close to *R. greyi* as to be considered conspecific by

some authors, he did not alter that opinion. In 1921, O. Thomas obtained
further material from Mt. Compass through the good offices of Professor Wood
Jones, then working in Adelaide, and after reviewing the series referred to *R.
greyi* in the British Museum, concluded that it was not homogeneous, and desig-
nated one of the former cotypes as a lectotype to represent Gray's species. This
specimen (B.M. 41, 1266) is stated by Tate (1951, 329) to be of the "Gould
Collection". At the same time, Thomas (*op. cit.*) described *Rattus culmorum
austrinus* from a specimen collected by J. B. Harvey, and donated to the Zoo-
logical Society of London in 1841. Harvey collected both on Kangaroo Island
and at Port Lincoln on Eyre Peninsula and the place of origin of the type of
austrinus is also quite uncertain, Thomas (1921) and Tate (1951) accepting
Kangaroo Island, and Iredale and Troughton (1934) and Ellerman (1941), Pt.
Lincoln. This dispute would have no relevance here were it not for the fact
that Tate (1951) has been brought to the conclusion that *austrinus* is a form of
R. greyi and not of *R. culmorum*. Troughton (1920) recorded the persistence of
the species (under the pseudonym *R. assimilis*) on both Kangaroo Island and
Eyre Peninsula.

A second insular representative was discovered by Wood Jones on Pearson
Isles in the Investigator Group of the Eyre Peninsula coast, and this was de-
scribed by Thomas (1923) as a full species, *Rattus murrayi*, but now more
generally regarded as *R. greyi murrayi*. Wood Jones (1924, 1925) gave an
excellent general account of both the mainland and island forms and provided
the first illustrations of the species. In 1936 Brazenor separated a western
Victorian population from the typical form under the name *R. g. ravus*; but this
being preoccupied by *Epimys ravus* (= *Rattus ravus*) of Robinson and Kloss
was replaced by *peccatus* by Troughton (1937); Tate (1940) independently
noted the preoccupation of *ravus* and suggested *brazenori* as a substitute. These
described forms have since been noted and discussed in monographic works on
muridae by Ellerman (1940-1949) and Tate, 1951. In spite of this consider-
able body of work it cannot be said that *R. greyi* is a well understood species.
Not only the vagueness in the provenance of early types, but still more, the
tendency to limit the basis of differential characters to the barest conventions
of museum systematics, renders the subspecific identification of material from
descriptions, a hazardous proceeding.

The local interest of *R. greyi* derives largely from its insular representatives
which are frequently the only mammals on the islets of the continental shelf
which can be obtained in numbers, and which if fully studied might give
valuable information on the post-Pleistocene history of this area. The immediate
origin of the present paper has been the necessity of assessing the degree of
differentiation which has been attained by an island population as compared
with one from the mainland, and in such work holotypes, however well de-
scribed, are of limited service if unaccompanied by data on topotype series
which can supply the key to the range of variation normal to the form they
represent. The correspondence or divergence of individual specimens of
closely related and intergrading forms may be largely a matter of chance,
but population trends, as shown by the frequency with which characters recur,
is likely to be much more significant of affinity.

Although several considerable series of *R. greyi* are stated to exist in col-
lections, both in this country and overseas, no adequate analysis of their charac-
ters is available for such a purpose as I have indicated. Between 1936 and 1939
during the course of field work by the writer in the Fleurieu Peninsula, chiefly
upon the associated species *R. lutreola*, a considerable series of *R. greyi* was
obtained as a by-product. This material, personally collected over a restricted

area and fully authenticated with field data, lends itself well in making good this deficiency, which forms the chief content of the sequel. The series is then used as a standard in a re-examination of other groups both insular and mainland, which are available here, and in addition, the distribution, status, and habits of the species are briefly discussed and some details given of its behaviour in captivity.

DISTRIBUTION AND HABITS

The present distribution of the species, as far as it is known, involves a narrow subcoastal strip extending from the Portland district of western Victoria to the southern portion of Eyre Peninsula in South Australia and some of its off-lying islands, and is thus almost entirely within the territory of the latter State. Its eastern extension in Victoria, however, may be considerably greater than is supposed, as it tends to be masked by the overlap with the very similar *R. assimilis*, the most westerly record of which appears to be at Beech Forest in the Otway Peninsula of Victoria.

The range thus interpreted is one of the most restricted for Australian rats, but if Tate's suggestion (1951) is adopted of considering *R. greyi* as a sub-specific south-western off-shoot of *R. assimilis*, the combined range is then probably the most extensive, the forms *R. a. coracius* extending to north Queensland and *R. a. manicatus* to the Arafura coast of the Northern Territory. The absence, so far as known, of any representative of the species group in Tasmania and the frequency of its occurrence on the islands of the South Australian coast, is a significant point in its distribution. Shortridge (1936) claimed *R. greyi* (as distinct from *R. fuscipes*) as a member of the Western Australian fauna, but this is not confirmed by Glauert (1950). Tate (*op. cit.*) suggests that such an extension was established during the last pluvial phase of the Pleistocene and has lapsed during subsequent dry times, but he was inclined to underrate the arid tolerance of modern *R. greyi* as shown, for example, by the dune colonies of Eyre Peninsula and some of its islands, and it may yet be found to extend much further along the south coast in this direction also.

In South Australia at the present time it is well established in the southern portion of the Mt. Lofty Range and on Kangaroo, Greenly, Pearsons, Nth. Neptune, and Gambier islands and probably on several other islets off the coast. It occurs much more sparsely in the lower South-eastern District and persists also in small numbers along the coastal portion of the Adelaide-Wakefield Plain and in the southern portion of Eyre Peninsula. The early obliteration both of fauna and vegetative cover by farming operations in large portions of lower South Australia, necessarily leads to a patchy, discontinuous distribution common to most local mammals at present, but how far this was true of the pre-European era and to what extent the present occupied areas were formerly linked, is largely conjectural. Its survival north of Adelaide, in sheltered, unutilized spots, such as the mangrove belts, suggests that it may formerly have occupied many of the timbered portions of the wheat lands of the Lower North and of Yorke Peninsula. It is absent from the major expanses of the Mallee, and sub-fossil records do not appreciably extend the existing distribution.

Today, in the hill tracts south of Adelaide, wherever sufficient cover has been left for its needs, it holds out in small numbers and seems able to survive the attentions of both the fox and domestic cat, and is one of the very few native mammals which are at all likely to be taken here by random trapping. Twenty years ago, before the use of trace elements led to a phenomenal increase of pasture and sheep breeding, the portion of the Fleurieu Peninsula south of the

watershed and including the valleys of the creeks between the Waitpinga in the east and the Tapanappa in the west, was an almost virgin wilderness and *R. greyi* was in very large numbers here and almost ubiquitous. It could be trapped with almost equal certainty on dry laterite ridges under stands of stringy bark timber (*Eucalyptus obliqua* and *E. baxteri*) and dwarf eucalypt scrubs or in the tangled jungly growth along the swampy heads of creeks; the former, however, and hill slopes with moderate cover of bracken and xanthorrhea were the more characteristic stations. In this area it had no marsupial competitors and few effective predators and the periodic bush fires which swept the creek valleys from the divide down to the sea were the only cause of large scale mortality. From these disasters, however, it made rapid recoveries and reoccupied the burnt country with remarkable speed. Its relations with *R. lutreola* which also has a firm hold on this country will be more particularly discussed elsewhere, but it may be remarked that it is a much more wide ranging and adaptable animal than the latter and only comes into competition with it in the immediate vicinity of the restricted *lutreola* colonies which are usually in damp areas near the creek beds or in wet swamps. Unlike the west Victorian and Kangaroo Island populations which make considerable living burrows in suitable soils the local form of the Fleurieu Peninsula does not normally burrow, but shelters in or under fallen logs and in matted banks of grass and sedges and dried fern. Even where very plentiful it is quite inconspicuous, leaving no well-defined runways and being seldom seen by day.

Some information on the feeding habits has been obtained by the examination of stomach contents of considerable numbers from the Fleurieu Peninsula; this consists most frequently of a dark coloured, finely ground pulp in which seed case fragments form the chief recognisable constituent. Incineration of the dried mass yields an ash rich in sand which gives colour to the view that subterranean materials are largely used for food. This had been inferred independently from the frequency with which the rat had been trapped on burnt clearings under timber where the soil was much scarred by fresh, shallow excavations. About one-half the stomachs contained appreciable quantities of insect material representing both Coleoptera and Orthoptera, and in two cases a fleshy mass derived, at least in part, from an Amphibian. No trace of green vegetation could be detected. The available evidence, therefore, suggests that in this district at least, seeds, roots and tubers are the chief elements of the diet, with a not unimportant intake of insects and small vertebrates. It is very easily trapped with a variety of baits of which bread, fat and sliced apple were found about equally effective.

The stomach frequently carries a heavy infestation of a nematode, identified by Mrs. I. M. Thomas as a *Physaloptera* species, and several unidentified ectoparasites occur, of which the most important quantitatively is a *Laelaps* species.

As regards reproduction, the data is scanty and the evidence mostly negative as the greater part of the Fleurieu Peninsula series was obtained at times when reproduction was largely suspended. However, by combining such information as it yields, both in the field and in captivity, with that from other South Australian mainland localities and from Greenly and Gambier Islands and western Victoria, it may be seen that, in the male, testes first undergo a sudden enlargement and become scrotal in site in July and August and may be found so till the following February; and that in the female activity in the form of observed littering of wild caught rats in captivity, and lactation and pregnancy in the wild, extend from September till February. While the evidence from any one locality is inadequate for a positive statement, the combined data might be

taken as indicating that the overall reproductive pattern for the species is one of activity from late winter or early spring to late summer (July-February) and that there is a period of quiescence in autumn and early winter (March-June). Vulval occlusion is absent in the Fleurieu Peninsula series and in other mainland material has been noted in one example only; a subadult from the Meadows Creek area, slightly north of the main series, in April. It is more frequent in a Greenly Island collection (*infra*). The number of litters per year is not ascertained. In the single littering observed in captivity four young were produced, but in western Victoria, six full-term uterine embryos were observed in two cases.

Numbers of *R. greyi* taken in the Fleurieu Peninsula were kept in captivity for varying periods under conditions similar to those described for *Pseudomys* (*Gyomys*) *apodemoides* in my paper of 1944. On a diet of mixed grain, potatoes and hard fruit, which was always present in the cages in excess of requirements, and supplemented by a small ration of egg, honey, powdered milk and fat bacon, it appeared to thrive and produced and reared young. Water was drunk sparingly when supplied, but is not essential, and two groups, one captive born and one wild, lived through a hot summer without it.

In general, it proved to be a vigorous, restless and aggressive little creature. The males made almost ceaseless attempts to escape and frequently succeeded by gnawing holes in the wire netting, but the escapees made little use of their freedom, seemed nonplussed by their enlarged surroundings and were usually easily retrapped in the vicinity of the cages. I cannot confirm Wood Jones' (1925) description of its "gentle" character. Its failure to bite when handled (which is not invariable) seems to be due to a paralysis of fear rather than to tolerance, and though it may not move away when touched, it frequently trembles, its tail beats an involuntary tattoo and its eyes bulge in their sockets. Impressions of temperament no doubt depend on the social balance of the communities observed. The groups which I have watched always contained an excess of males and under these conditions it appears in a very different light. Its libido during the season is quite insatiable and under stress of sexual competition it wages relentless war on all rivals real or potential and either kills or incapacitates them or enforces a recognition of its dominance. New additions to the colony were always treated with hostility though they all came from a very restricted area of the Peninsula. On at least one occasion house mice straying into the cage were killed and eaten.

Natural vegetation from the site of capture was used to carpet the cages and hollow logs and nest boxes were provided for shelters; these were generally occupied by pairs, but solitary males often made grass nests for themselves in the corners, either of an open cup-shaped form (Pl. 2. Fig. A) or a much larger domed structure, with an entrance near the base (Pl. 2. Fig. B). Much time and labour were expended in constructing these nests, which are not just random heaps of material, but were made by interweaving selected stems. They were demolished and rebuilt at frequent intervals, and nest building is evidently an important natural industry of the species. Transference of a group to a new cage was always followed by a tremendous burst of activity, all crannies and furnishings being examined in minute detail and moved if possible. At such times it ventured out freely in daylight, but ordinarily its activities were strictly nocturnal. It gave no evidence of any special climbing ability, and though it clambered about the netting on occasion, it made no use of the perches provided. The voice is much in evidence in young animals, but adults are rather silent, except when fighting or threatened, when they squeal harshly. The ectoparasite *Laelaps* sp. which is almost always normally present

in the wild, tends to increase unduly in captivity but may be checked by frequently dusting with pyrethrum.

The following serial notes cover some points of general interest in the development of a litter in captivity. The female, having left her mate and begun to make a nest separately, was transferred alone to a smaller cage, where four young were born next day (September 8) at unascertained intervals. They were uniformly pink on all surfaces and smooth and very vocal, using a shrill bird-like call when left in the cold by the mother. If disturbed at the nest she frequently jumped out, dragging some of the young with her, but they did not adhere firmly to the nipples. The female had but four of the ten mammae functioning – two inguinals and two pectorals.

At 5 days: The young were removed from the nest, examined and weighed, using a stoppered weighing bottle; weight 5 g. They were now perceptibly darker above than below and wrinkled; the mysticial vibrissae quite apparent and all white. When returned to the nest, the young were immediately flung out by the mother and rolled to and fro on the grass of the floor with her hands for a minute or more. She then took them in her mouth and carefully replaced them in the nest. This decontamination rite was frequently, but not invariably, carried out on future occasions of handling.

At 9 days: Dorsum now much darker than ventrum and completely clothed in a fine lead coloured down which is tinged with yellow on nape. The nestlings were vigorous but not capable of locomotion.

At 12 days: All young weighed 8 g.; pelage considerably advanced, the yellow areas extending nearly to the rump and on the outer aspect of the fore-limb a conspicuous patch of lead coloured underfur has appeared. Though still blind they could now scramble slowly over a bench. The three males were recognisable by minute paired spots of pigmented epidermis on the scrotal sites.

At 16 days: Pelage now markedly thicker, but of the same length and covering all the trunk and limbs but not the ears nor tail. The young were able to remain balanced on all four limbs and to walk an inch or two.

At 19 days: Weight 10 g.; furring of body and appendages complete; on the tail both scutation and hairs were apparent and its dorsal surface distinctly darker than below; dorsum of the pes haired with pure white on the toes only, that on the metatarsal area being slightly darkened at base. The soles of the pes were now darkened to a pale slate colour, but the palms of the manus, pink.

At 4 weeks: Eyes opened on the 22nd day. When removed from the nest the young jumped freely and ran and climbed about the cage and when handled made determined attempts to bite; the lower incisors were still white.

At 5 weeks: ♂ 13 g.; ♂ 11 g.; ♂ 13 g.; ♀ 13 g. The pigmented scrotal sites are still conspicuous and in the female there is no vulval occlusion. Though they were not seen to voluntarily leave the nest they undoubtedly do so at night and are taking solid food freely. Both upper and lower incisors were now yellow, but the former much darker. On the 34th day one of the 13 g. males was found dead; head and body, 73; tail, 60; pes, 20; ear, 15·5 × 10; rhinarium to eye, 12; eye to ear, 12; skull greatest length, 25·6. The third molar had not yet erupted.

At 6 weeks: Another male found dead and partly eaten; the survivors weighed ♂ 14 g.; ♀ 16 g.

At 9 weeks: ♂ 23 g.; ♀ 33 g. The young had not been under close observation since last weighing and the remarkable disparity in size was quite unexpected; the male appeared to be entirely normal and healthy and active but was much less bulky than the female. Areas of exposed epidermis were still relatively unpigmented and when exposed to sunlight or handled, the light

coloured parts of manus, tail, pes and rhinarium, but not the ears, became deep pink. They were still comparatively leggy and awkward; they climbed about the netting more than adults but showed no agility at it. The male, having given evidence of rut, the dam was removed from the cage.

At 10 weeks: ♂ 30 g.; ♀ 38 g. At this time the pair made a grass nest exactly as fabricated by the wild born rats, and shared it. Regular observation and weighing had to be abandoned at this point, but in the next six months the young weathered their first summer successfully on the standard diet and without water. They were somewhat tamer than wild caught specimens, but the male always attempted to bite when handled. The pelage was now generally similar to that of the duller coloured adults, but less dense and glossy, and with fewer guard hairs and correspondingly reduced grizzle.

At 37 weeks: The female was found dead, having delivered four premature young; head and body, 136; tail, 130; pes 27·5; ear, 19 × 11·5; weight 80 g.; these dimensions are still somewhat below the approximate means of adult wild females, as selected by molar wear in the sequel (*infra*).

The surviving male was mixed in with a wild caught group of both sexes, but after resisting steady persecution for six months with varying success, he was removed to a cage of his own where he outlived the entire colony, dying during a heat wave on January 13, 1939, when day temperatures rose to 113 deg. in the shade; head and body, 151; tail, incomplete; pes, 27; ear, 20 × 12; wt., 145 g.; skull greatest length, 35·1. These values for head and body and weight exceed the approximate means of the adults of the wild caught series, but some others, notably the pes, are much lower, though all fall within the range except the weight. This exceeds the maximum for the wild caught group by 30 per cent. and was due to excessive fat. The skull length barely attains the minimum for the wild "adult" group subsequently measured (*infra*).

The death of this male at two years four months of age was almost certainly premature and probably due to heat apoplexy. Though the skull characters may have been modified by captivity, they do not suggest an aged condition, when compared with the oldest of the wild series. A life span for the species in nature of three or four years seems probable.

2. DEFINITION OF A STANDARD POPULATION OF
R. GREYI GREYI GRAY, 1841

The material examined below, which is later used as a standard series for assessing the status of other populations, was taken near the heads of the Callawonga, First, Boat Harbour, Tapanappa and Blackfellows Creeks in the Fleurieu Peninsula at the southern extremity of the Mt. Lofty Range. That it may be accepted as representative of the primary subspecies is indicated (within the limitations inherent in such comparisons) by the consonance of the lectotype with the range of variation now described and by the specific statement of Thomas (1921), that Wood Jones' donation from Mt. Compass was in agreement with the lectotype; this locality being but a few miles north in the ranges and presenting very similar ecological conditions to those of the drainage of the creeks named.

A strict interpretation of the term "vicinity of Adelaide" might put the type locality on the coastal Adelaide-Wakefield plain, which has some claim to be considered as a distinct natural region, differing from the highlands fifty miles to the south, which yielded the present material, in lower rainfall, higher mean

temperatures and, of course, in soils and vegetation. As will be shown later, the few specimens which are certainly known from this plain, show slight differences, and give colour to the view that the type locality lies in the Hills district to the south.

The Fleurieu series comprises 45 individuals representing an adequate range of sexual, seasonal and age phases; approximately one half of it is in the form of skins and skulls, with the remainder alcohol preserved. The sex ratio is 23 ♂ : 22 ♀ .

(a) EXTERNAL CHARACTERS

Size small; the phase of the species under consideration being one of the smallest of Australian rats. Limbs and appendages slender and delicate and the body build light and gracile, the dumpiness, which has been remarked (Wood Jones, 1925), being due to posterior lengthening of pelage rather than to a somatic character. The head (Pl. 3, Fig. A) is relatively large in comparison to body length and general bulk and has a well arched profile and but medium rostral development. The ear is thin in substance, bluntly rounded and carried conspicuously free from the head fur. The eye is large and prominent, and under emotional stress is capable of a remarkable degree of protrusion.

The *facial vibrissae* are relatively very strongly developed in *R. greyi*; all sets are well represented and the mysticials, genals and supraorbitals in particular are very long though slender bristles with extremely attenuated tips. As they are much subject to shortening by abrasion and breaking, the lengths quoted have been taken from a selected group of apparently undamaged examples, and except for the mysticials which alone have been used comparatively, the maximum observed length only is quoted. The counts have been made on fully furred examples, which in the case of the smaller bristles, present more difficulty than in earlier nude or part furred stages, so that these numbers are subject to correction.

In the *mysticial* set, the shorter, anterior, members are white for the greater part of their length, the remainder blackish brown with white tips; length in adults ranges from 42-53 with an approximate mean of 46·7; the three longest examples were supplied by males, but the mean for females is almost as high (46·0 cf. 47·4). The *genal* set is most frequently reduced to a single bristle, but rarely two of almost the same length and set very closely together, may be present; maximum 29 mm. *Supraorbitals* apparently normally two, though only a single bristle survives in some and a third very small member may be present in others; these, with the genals, have the same colour distribution as the longer mysticials; maximum 32 mm. A *postoral* papilla is strongly and consistently developed at a site about 6 mm. behind the oral canthus and supports three bristles, the longest (to 14 mm.) being dark at base and white tipped and the other two entirely white. The *submentals* are often difficult to delimit as a median group since numerous irregularly disposed bristles extend from the midline across to the angle of the mouth, where they are often longer than on the name site; the longest noted was 7 mm. and all are white to base. The *interramals* are also difficult to define in furred material owing to a tendency of the median papilla to break up into two or even three separate papillae, each provided with sensory hairs so that a total of six or more may be present; the largest complement noted on the median site was four, and the maximum length 14 mm.; these, like the submentals, are all white to the base.

The *manus* (Pl. 3, Figs. C and D) is slender and narrow, with a length from the base of the metacarpal pads to the summit of the apical pads (excluding

claw) ranging in fully adult examples from 13·0-14·0 mm. and the breadth transversely across the palm from the base of the 2nd digit from 4·5-5·0 mm. yielding an approximate mean breadth/length ratio of 0·37; the 3rd digit to 5·5 mm. and its claw to 2·5 mm. as maxima. The digital formula (length only) is $3 > 4 > 2 > 5 > 1$ but $4 > 3$ occurs rarely, and the 4th digit is always the stoutest. The claws are moderately developed, yellow horn coloured and with a free projection about equal to the apical pads and lightly fringed with bristles. The pollex is relatively well developed and its nail is large and conspicuous dorsally. The general colour of the palmar surface in life is pink; the central portions are deeply creased but not punctate nor granular. The grooves of the palmar surface of the digits are deeply incised and the 4-5 semi-annular ridges which they enclose are prominent and entire distally, but the proximal two are commonly broken up into scales, in a more decided fashion than is usual in Australian *Rattus*.

The *palmar pads* are smooth and rounded in outline but are relatively large and with bold relief; the surfaces are feebly striate. The interdigitals are mounted on prominent folds of integument which in available illustrations (Wood Jones (1925), Brazenor (1936) *op. cit.*) are not always distinguished from the pads themselves, so that very different conditions appear to be attributed to the species. The metacarpals vary considerably in shape and area and have extensions on to the lateral aspects of the manus, which complicate the overall appraisal under these heads. The outer metacarpal (hypothenar) is always the longer and extends lower towards the carpus and in palmar aspect is usually twice as long as broad, and a pointed oval in shape. The inner metacarpal is shorter and broader and is sometimes equal and rarely greater in area than the outer; its palmar portion is roughly an inverted U or bell shape, with a depression between the arms and an accessory fold on the lateral aspect towards the pollex, separated from the main portion by a distal notch. The interdigitals are somewhat more constant, the most frequent shape being an inverted broad piriform for the median pad and inverted cardiform for the 1st and 3rd. The 3rd interdigital has a small circular satellite pad at its postero-external angle with a frequency of about 90 per cent., which, however, may be reduced to a dependant heel or disappear altogether. In point of area the prevailing pad formula is: outer metacarpal > inner metacarpal > 2nd interdigital > 3rd > 1st[1], but as shown above the metacarpals may be equal, or the inner the larger.

Neither median antebrachial nor anconeal vibrissae were traced on the forelimb in the available material; the ulnar carpals are 4-5 in number, arranged in two groups, and are pure white to base with the longest of the set reaching 13 mm. as a maximum.

The *pes*, relative to head and body length, is one of the longest amongst Australian species of *Rattus*, with an approximate mean value in adults of 19·7 per cent. of the head and body, and also one of the narrowest, the ratio of breadth across the sole from the base of the 1st digit, to the length, averaging about 0·22. It tapers gently for most of its length and has a well constricted calcaneal portion; the 3rd digit reaches 7 mm., its claw 3·5 mm. and the hallux 4 mm., as maxima. The digital formula is as in the manus and the 4th digit again usually the stoutest; the claws sharp and delicate, coloured as in the manus, but with longer fringing bristles which may exceed them by their own length. Digital rings increased to 6 on the 2nd, 3rd and 4th and all except the distal member divided into 2 (or basally into 3) large scales. The colour

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[1] The 2nd of the primitive pentadactyl manus.

of the sole is pale pink with the central portions sometimes darkened with an infusion of slate, which, however, does not extend to the pads.

The *plantar pads* are strongly developed and more definitely striate than in the manus. The inner metatarsal in this series is notable in being broader than usual and generally lacks the long, drawn-out, comma-shaped tail, common in the genus; in shape it is an irregular oval narrowing proximally but with its maximum breadth often more than half its length. The outer metatarsal is broad oval or nearly round and only one-quarter or less of the area of the inner. The median interdigitals are regularly piriform and the laterals inverted cardiform; the 1st with a slight depression towards the heel, and the 4th with a distinct separate satellite pad at the postero-external angle in 50 per cent. of cases only; in the remainder, it may be represented by an accessory fold or heel or be entirely absent (20 per cent.); much more rarely a heel or satellite may appear at the base of the 1st interdigital. In adults, the most frequent size relation is: inner metatarsal > 3rd interdigital > or = 2nd > 4th > 1st > outer metatarsal; this accounts for 85 per cent. of cases, but it is characteristic of the species that the lateral interdigitals are large with respect to the median and a condition of subequality between all four may be reached; in two cases the median interdigitals are larger than the inner metatarsal.

Calcaneal vibrissae were not traced.

The *tail* is slender and gently tapered, with attenuated apex and no terminal expansion. The relation of its length to that of the head and body ranges from 85-110 per cent. with an approximate mean of 94·3 per cent. In the group of seven species which have been chiefly used in these comparisons and comprising *R. greyi, assimilis, lutreola, villosissimus, colletti, norvegicus*, and *R. alexandrinus*, this mean is exceeded by the latter alone. In the entire series of *R. greyi* from the Fleurieu Peninsula, the length of tail equals or exceeds that of the head and body in about 24 per cent. of cases and the distribution of the frequency of this relation shows only slight differences between ♂ and ♀ (26 cf. 21 per cent.) and adults and subadults (22 cf. 25 per cent.), so that the variation in this feature is very largely an individual one. Scale counts were not made upon animals in the field, but as the range observed in alcohol preserved material and in filled skins is identical, it is probable that the results obtained are characteristic of this form. The middorsal count in adults ranges from 12-14 per cm., 13 scales having the highest frequency (54 per cent.) and 14, 38 per cent. Proximally, the dorsal count averages slightly less, while distally it may rise as high as 21 per cm. at the apex. In subadult and immature phases the count is decidedly higher, the middorsal number ranging from 13-15 per cm. with frequencies of 44 per cent. for 15 scales, 31 per cent. for 14 and 25 per cent. for 13. The number of hairs per scale is normally three, but shows considerable irregularity dorsally, especially towards the base, where it may vary from one to three. The length of tail hairs is from 2-2·5 scales middorsally and increases distally. The tail is decidedly darker above than below in a large majority of specimens, both scales and hairing contributing to the effect, but the degree of the difference varies widely and it may be almost as pale above as below, but is never darker below. Light coloured epidermal markings, possibly traumatic in origin, are sometimes present and rarely as much as 20 mm. at the apex may be entirely white, both as to epidermis and hair.

The *mammary formula* in lactating females examined is 2-3 = 10, but in subadults or quiescent adults, the nipples are very completely retracted and in many of these the pectoral and sometimes the thoracic as well, could not be traced by ordinary macroscopic examination under a lens, but whether they are completely suppressed as implied by Wood Jones (*op. cit.*) remains to be

shown. As mentioned above, in a female lactating in captivity for four young, only four of the ten were functioning; two pectorals and two abdomino-inguinals. The pectoral and thoracic nipples lie respectively just in advance and just behind the insertion of the forelimb and upon lines which diverge posteriorly, the thoracic being always more laterally sited. The abdomino-inguinals show considerable variation in pattern due to changes in both the lateral and antero-posterior intervals separating them. An evenly-spaced crescentic arrangement (Text Fig. 1 A) is frequent, but a rectilinear form in which the 2nd and 3rd
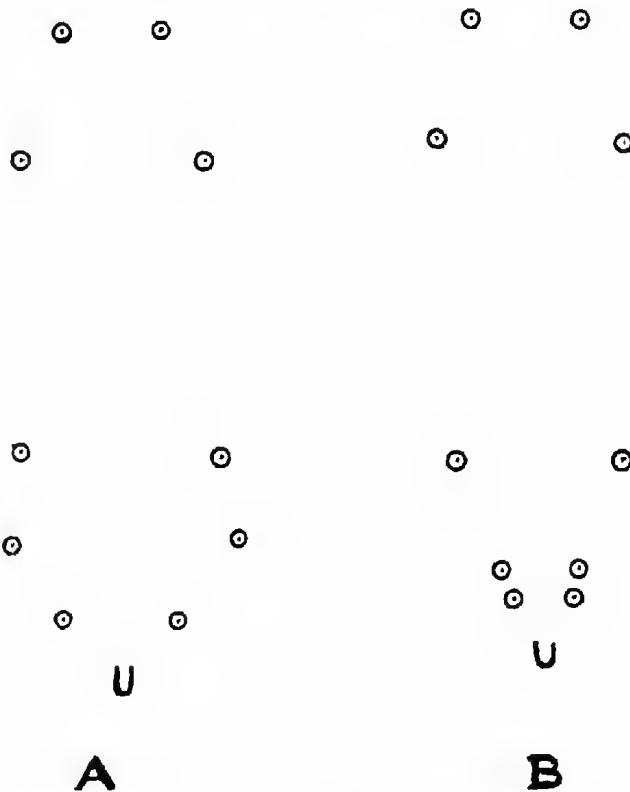

Fig. 1.
Diagram showing extremes of variation in the mammary
pattern of *R. greyi greyi* (x 1·0 ca.).

are nearer both to the midline and to one another, than to the 1st, also occurs (Text Fig. 1 B) as well as intermediate conditions. The B pattern is apparently that noted by Tate (1951) in the form *R. g. peccatus* from West Victoria. The intervals represented in the diagrams were measured with the limbs extended laterally to the maximum. The first (lower abdominal) lies well in advance of the insertion of the hind limb.

The *testis* is relatively very large and at its maximum development in the scrotum has diameters of 23 and 14 mm. approximately and weighs about 2 g.; it is as large as in the much bulkier *R. lutreola* of the same habitats, but a more squat oval in shape. The scrotum is well furred except at the caudal extremities, which are nude and have the epidermis pigmented dark gray. The epidermis of the perineal site in the female is also darkened slightly, but the pigment is

diffused and not concentrated on the two distal sites as in the male. In adults the genital tubercle has a free projection of about 8 mm. in both sexes.

Sexual variation in external characters except where noted in the account is slight or largely obscured by individual variation.

(b) DIMENSIONS

The four chief dimensions quoted were obtained as follows: *Head and body*—This is the total length of the dorsal contour, minus the tail length. *Tail*—The length of the ventral surface of the tail from the posterior margin of the anus to apex of the last vertebra, excluding the terminal hair. The measurement is made with the tail flexed at right angles to the body. *Pes*—The length of the plantar surface from the extremity of the heel to the extremity of the most distant apical pad, excluding the claw, the digits being straightened and in line with the metatarsal. *Ear*—Length from the lowest point of the tragoid notch to the apex of pinna.

The figures give the range and approximate mean for two overlapping age groups; (1) an adult plus aged group of 10 males and 6 females in which all molar crowns have sustained sufficient wear to obliterate the pattern of individual cusps and replace it by one of transverse lophs and in which rostral development is marked and the zygomatic outline untapered, and (2) an advanced subadult group of 9 males and 13 females in which all cusps show appreciable wear and the rostral development is less. In the adult group the range and approximate mean of the percentage relation of length of tail, pes, and ear, to that of head and body, follow the absolute dimensions. Head and body and tail are to the nearest mm.; others to the nearest 0·5 mm.

1. Head and body, ♂ 138-159 (146·7), ♀ 139-155 (145·0); tail, ♂ 130-153 (139·7), 84·7-110·0 (96·1) per cent., ♀ 127-146 (134·6), 83·9-104·0 (92·5) per cent.; pes, ♂ 27-32 (29·3), 17·2-22·2 (19··9) per cent., ♀ 28-28·5 (28·2), 18·1-20·1 (19·4) per cent.; ear length, ♂ 20-22 (21·1), 13·3-15·8 (14·3) per cent., ♀ 19-21·5 (20·2), 13·1-14·6 (13·9) per cent.; ear breadth, ♂ 11-13·5 (12·2), ♀ 11-13 (12·1); rhinarium to eye, ♂ 17-19 (18·4), ♀ 16-19 (17·9), eye to ear, ♂ 13·5-16 (14·5), ♀ 14-16 (15·1); weight in grammes, ♂ 80-112 (92·7), ♀ 70-90 (82·6).

2. Head and body, ♂ 120-146 (131·8), ♀ 122-145 (131·8); tail, ♂ 115-137 (125·0), ♀ 115-135 (123·2); pes, ♂ 27-30·5 (28·5), ♀ 26·5-29 (27·8); ear length, ♂ 19-21 (19·7), ♀ 18-21 (19·7); ear breadth, ♂ 10-14 (11·9), ♀ 10-13·5 (11·8); rhinarium to eye, ♂ 16-18 (17·0), ♀ 16-18 (16·9); eye to ear, ♂ 13·5-15 (14·1), ♀ 13-15 (13·8); weight in grammes, ♂ 56-85 (67·4), ♀ 51-75 (65·7).

Though there is a wide overlap in all dimensions between the sexes, it would appear that in fully adult animals, the female is approximately equal to the male in head and body length, but is decidedly lighter when non-pregnant (10 per cent.) and averages slightly shorter in pes, ear and tail. The enormous example quoted by Wood Jones (1925, 304) with a head and body length of 186 mm. has no near counterpart in this series. The very low foot length of 26 mm. associated with it, suggests that the former may be a typographical error.

(c) PELAGE

The pelage is fine and soft and in prime condition is dense and copious and middorsally consists of three piles: (1) a fine silky underfur of nearly uniform diameter and 18 mm. long; the basal two-thirds is a deep slate (near Ridgway's

dark plumbeous) and the terminal one-third is broken up into three colour bands, successively dark brown black, a bright tan between ochraceous tawny and ochraceous orange, and the extreme tip again brown black; this pile is both quantitatively and chromatically the most important element in the pelage; (2) a second pile may reach 25 mm. in length and is made up of much smaller numbers of hairs with flat shafts which broaden in the upper third of their length; they are plumbeous at base, but with the terminal 6 mm. brown black and the extreme tip buff or ivory; (3) a sparse admixture of guards which reach 35 mm. in length and darken from plumbeous to brown black over their distal half. Posteriorly the three sets of hairs may lengthen to 20, 30 and 45 mm., respectively, and over the rump and sides an increasing proportion of the latter are tipped with white or ivory.

The general colour effect dorsally is a fine almost uniform grizzle of rich tan, brown black and buff or ivory which almost entirely obscures the basal slate colour and when viewed from a little distance approximates to Ridgway's cinnamon brown in the warmest and lightest coloured individuals, and to bistre in the coldest and darkest.

The sides are lighter than the back owing to a progressive weakening of the subterminal band to a buffy brown and reduction in the overlay of black tipped guards, but in most individuals the lateral surfaces remain distinctly grizzled and the passage to the pale ventrum is abrupt. Mid-ventrally, there are two piles; an underfur 10 mm. long with its basal 8 mm. a somewhat lighter plumbeous than dorsally and with the tips greyish white or pale buff and a sparse intermixture of guards 15 mm. long which are slate with the distal flattened 5 mm. white or near white. The basal slate shows through more than on the dorsum and the general colour here is a greyish white with a more or less decided wash of yellow or buff over the belly. Gray (1841) singled out this variation of the yellow tone of the ventrum in his original description; but in the whole of the present series it is appreciable and sometimes decided over the mid-belly, while the throat, chest and perineal areas may remain grey white. In a few examples there is an invasion of the belly area just in advance of the insertion of the hind limb, by the buff or brown of the sides.

The facial areas and crown are paler and more buffy than the back, though still well grizzled. The ear backs in dried material are usually darker than the head, chiefly owing to the blackish pigmentation of the epidermis, the very scant hairing being a pale brown externally and greyish white internally — in a small proportion, however, greyish ear backs lighter than the head are present. The outer aspects of the forelimb are greyer than elsewhere — about Ridgway's light drab, and long haired, and just above the carpus a conspicuous dark brown black marking is constantly developed, sharply contrasted with the silvery white carpus and manus; the hairs of the latter, however, are usually pale brown at base and there is sometimes a very slight grizzling of all-dark hairs over the metacarpus. The outer aspects of the hind limb are brown like the sides, with a slight darkening above the calcaneum sometimes developed, and with the dorsum of the pes as in the manus.

The tail is thinly clad with short hairs closely adpressed mid-dorsally and then lifting and lengthening slightly distally. In unfaded pelage, the dorsal surface is decidedly darker (both as to hairs and epidermis) than the ventral — the mid-dorsal hairs being near bistre darkening to near black at the apex, while on the sides and beneath they are greyish white proximally and various shades of weak brown, distally. However, as mentioned above, as a result of what are no doubt periodic changes in each individual, dark strongly bicolor tails and others which are equally pale on all surfaces, may be seen at all seasons.

Variation of a strictly individual kind is well shown by the series and may be seen in examples of equally fresh and copious pelage, trapped at the same time on the same site. In such cases it is due chiefly to marked differences in the tone and length of the subterminal band of the first pile and to the length and profusion of the black overlay of the second and third – the white tips of the latter are too sparse to have appreciable effect. In examples with a short subterminal band of relatively weak colour (ochraceous buff) with a heavy overlay of second pile and guards, dark blackish brown scarcely grizzled coats result, whereas, with a broad richly coloured band of ochraceous orange and few guards, the coat becomes strongly rufescent and appears markedly grizzled.

In addition to these individual differences, there are others due to progressive fading and delapidation of the pelage, resulting in a general weakening of the colour and a change of hue, caused by the showing through of the slate basal colour zone of all three piles. This leads to pale fluffy coats of a slightly avellaneous tinge, approaching wood brown, which is also more or less characteristic of early immaturity. I am of opinion that this phase has unduly influenced some existing descriptions of the species. Wood Jones, for example, in emphatically repudiating Ogilby's (1892) description, states that there is no "intense reddish" anywhere in the coat and that the smoky colour of the under-fur shows through and subdues the whole. This, however, is not true of the pelage at its best as described above, and it would be difficult to avoid the terms "red brown" and "blackish brown" in ordinary parlance, in defining such.

Although the area has a hot summer and comparatively sharp winter with marked difference of mean day temperatures in February and July, seasonal differences in the pelage are at a minimum. While the richest pelage of the series was taken in August others of almost equal quality were seen in February and May, and conversely, worn, short and faded coats were obtained in all three months. The time of renewal of the coat is evidently an individual matter independent of seasonal conditions and following a cycle determined largely by the time at which the rat was littered. No evidence of an orderly moult proceeding successively over different areas of the surface, with well marked boundaries between the old and new coats, could be detected; but in two individuals taken in May, large areas of both dorsal and ventral surfaces, simultaneously, showed a short replacing coat mingling with the base of the main pile.

No valid sexual differences in pelage could be traced.

(d) CRANIAL AND DENTAL CHARACTERS

Twenty skulls, all extracted from animals of known external characters and dimensions, have been examined and measured.

The skull (Pl. I, Figs. A-D) is notable for its smoothly rounded outlines and weak muscular impressions, which are retained without appreciable alteration into advanced age. This gives it a distinctive appearance which at once marks it off from other Australian species of *Rattus*, and recalls somewhat the form of the larger species of *Pseudomys s.s.*

The muzzle is of moderate length but very narrow and with a marked tendency to parallelism of its sides. The maximum width of nasals is always subterminal, but fluctuates over a 20 per cent. range, with corresponding variation in the overall shape of the bones which, however, never develop an abrupt or bulbous expansion. The fronto-nasal suture is usually broad and square and the premaxilliary process may overlap it posteriorly or fall short. The zygomatic outline is broad with some flattening at the mid point of the curve and with

the maximum width always at the squamosal root, but in adults the middle width is almost as great and it is only in distinctly subadult skulls that there is any appreciable posterior taper of the arch. The interorbital region tends to be tubular and smooth, and the supraorbital margins are not ridged. The brain case is broad and smoothly rounded and temporal crests are only slightly developed or even quite absent. The lacrymals are large, and the anteorbital fossae, though variable, are never strongly developed and are sometimes conspicuously small.

In lateral aspect the dorsal profile is well arched but less so than in such forms as *R. culmorum* and *R. lutreola*. The zygomatic plate is shorter vertically than in *R. assimilis*, but is otherwise similar and its anterior margin may be either strictly vertical or with a slight concavity at base. Conflicting statements have been made about the size and shape of the anterior palatal foramina in *R. greyi* and their relation to that of *R. assimilis*. In the present series the adult condition is that length is comparatively constant and always decidedly greater than the molar rows, but width (like that of the nasals) is one of the most variable of dimensions, with a range of 15 per cent. or more — however, in relation to such species as *R. culmorum* and *lutreola* they could only be described as wide, and though the exact shape is variable, their combined aperture does not narrow posteriorly at all markedly as in *assimilis* and is sometimes as wide posteriorly as in the middle. The bullae are small with their length about equal to that of the molar rows, but they are relatively broad and well rounded.

Age changes in the skull are less marked than usual, but can generally be recognised in the change in shape of the zygomatic arches above mentioned and in the elongation of braincase and rostrum. Sexual differences are inappreciable in the subadult group; in that of adults the largest example is from a very aged male and is disproportionately enlarged in relation to its somatic dimensions — whether females equally enlarged occur, the material is insufficient to determine.

In the molars (Pl. 1, Figs. E and F), small but distinctly developed anterior cingular cusplets can be made out on M^1 in about one-third of the immature skulls and vestiges of them persist in one or two adult dentitions. The buccal element (T.3) of the first lamina of the same tooth is usually very completely suppressed but is weakly indicated in a few examples. In the lower molars the interproximal accessory cusps of M_1 and M_2 are always present in unworn teeth, but are often very small and are frequently eliminated from the adult dentition by wear. The rate of molar wear is subject to much irregularity owing, no doubt, to varying amounts of earthy abrasive ingested with the food, and the crown pattern by itself is only a very rough guide to age. There are several examples in the series of distinctly immature animals judged by somatic and cranial characters, in which the cusps of all the laminae are transversely linked by broad bands of dentine.

The following figures give in turn the range and approximate mean of the skull measurements and molar rows for (1) five males and two females in the adult group as defined (*supra*), and (2) five males and four females in the subadult group:

Greatest length, ♂ 35·7-38·7 (36·7), ♀ 35·8-36·9 (36·3), ♂ 33·0-35·0 (33·7), ♀ 32·6-34·3 (33·6); basal length, ♂ 31·0-34·3 (32·3), ♀ 31·6-32·5 (32·0), ♂ 28·6-30·1 (29·1), ♀ 28·5-30·4 (29·5); zygomatic breadth, ♂ 17·5-18·9 (17·9, ♀ 18·1-18·2 (18·15), ♂ 16·9-17·5 (17·0), ♀ 16·3-17·2 (16·9); interorbital breadth, ♂ 5·0-5·7 (5·4), ♀ 4·8-5·1 (4·9), ♂ 5·0-5·5 (5·2), ♀ 5·0-5·0 (5·0); nasals length, ♂ 13·2-14·5 (13·8), ♀ 13·8-14·0 (13·9), ♂ 12·2-13·0 (12·6), ♀ 11·6-12·7 (12·1); nasals greatest breadth, ♂ 3·3-4·1 (3·5), ♀ 3·8-3·8 (3·8), ♂ 3·2-3·9 (3·6), ♀ 3·3-3·5 (3·4); palatal length,

♂ 18·6-20·5 (19·3), ♀ 19·2-19·2 (19·2), ♂ 17·5-18·1 (17·8), ♀ 17·3-18·2 (17·7); anterior palatal foramina, length, ♂ 7·2-7·5 (7·3), ♀ 7·3-7·3 (7·3), ♂ 6·5-6·8 (6·7), ♀ 6·5-7·0 (6·6); *ditto*, breadth, ♂ 2·3-2·7 (2·5), ♀ 2·3-2·4 (2·35), ♂ 2·0-2·4 (2·2), ♀ 2·0-2·3 (2·2); bulla, length, ♂ 6·1-6·7 (6·3), ♀ 6·0-6·1 (6·05), ♂ 5·8-6·3 (6·0), ♀ 5·8-6·3 (6·1); Ms.[1-8], ♂ 6·2-6·3 (6·26), ♀ 5·8-5·9 (5·85), ♂ 5·8-6·3 (6·1), ♀ 5·9-6·3 (6·1).

3. OTHER POPULATIONS OF *R. GREYI*

(a) MAINLAND DISTRICTS NORTH OF FLEURIEU PENINSULA

A group of ten specimens from hill tracts north of the Fleurieu Peninsula in the valleys of the Sturt and Onkaparinga, offer no appreciable distinction from the standard series. Two examples are slightly shorter tailed and another gives an extralimital value of 58 mm. for mysticial vibrissae.

Three female specimens from a mangrove swamp near the mouth of the Gawler River about 20 miles north of Adelaide on the Adelaide-Wakefield plain in a very different environment from the Hills series, are of interest as showing the first signs of significant differentiation. While in full agreement with the standard series in external characters and pelage, they carry the shortening of the tail a stage further (min. 78 per cent.) and are longer footed (29-29·5 mm.). One of them provides the largest female skull from the South Australian mainland, measured (greatest length 27·3) and the anterior palatal foramina are longer and narrower (7·5-7·6 and 2·1-2·1), and the molar rows just below the lower limit of the range (5·7-5·8) and the individual teeth narrower than in the standards.

I have no relevant material on which to base an independent opinion as to the extent of the westward extension of *R. greyi greyi* on the mainland, but both Iredale and Troughton (1934, 72) and Tate (1951, 329) record it from Pt. Lincoln on Eyre Peninsula. Tate's position in so doing was only made tenable by his willingness to accept Kangaroo Island as the type locality of the form which he regarded as *R. greyi austrinus*. But the few specimens from Kangaroo Island which I have examined convince me that the form of *R. greyi* which occurs there does not represent *austrinus* as defined by Thomas, and is, in fact, very doubtfully separable from the typical Fleurieu race on the opposite shore of Backstairs Passage.

In spite of Thomas's assumption that his *R. culmorum austrinus* was "a common form in South Australia in the 1840's", it does not seem to have found its way into any local collections, and its origins are as obscure as when described. But whether it came from Kangaroo Island or Eyre Peninsula, or formerly occurred on both, its place, on a basis of described characters, seems to be definitely with *culmorum* and not *greyi*, and it is not further considered here.

Tentatively and as a working hypothesis I accept the above opinion on the range of *R. greyi greyi*, but the Gawler River specimens suggest that the case may have been less simple than that.

(b) GREENLY ISLAND

This site is a steep granite ridge with a peak of 750 feet at the eastern end and two semidetached masses at the western end, lying about 19 miles west-south-west of Point Whidbey on the west coast of Eyre Peninsula. The

greater part of the island surface consists of unbroken rock slides, but near the summit and on the south slope where some remnants of the original limestone capping persist there is a stunted forest of *Casuarina stricta* trees and thickets of the same species in bush form, together with *Melaleucas*, and *Correas* occur on broken areas of the north slope. There is a considerable small flora in suitable localities where soil has accumulated, including such genera as *Atriplex*, *Rhagodia*, *Frankenia* and *Calandrinnia*.

The island is uninhabited and seldom visited. The writer made a six days stay there in November, 1947, to investigate the local wallaby, tracks of which had been seen by Wood Jones (1923), and found a form of *Rattus greyi* abundant on the main mass of the island. It apparently does not burrow and there are few parts of the island where it could indulge such a habit except on a very limited scale, but there is ample ground cover in debris under the she-oak timber and in the denser thickets and it evidently camps in such shelter and in rock crannies. It is much less sophisticated and shy than its mainland relatives, and was frequently seen foraging about in the more open parts in the late afternoons and at night it invaded the camp in numbers and could be freely inspected in a torch beam at a distance of a foot or so — in the beam the eye is blood red. It was extremely noisy, ransacking all camp gear and sampling all provisions left unprotected. Although it must of necessity be largely vegetarian, it showed a strong partiality for flesh foods at the camp and mutilated wallaby carcasses left there. The stomach contents of those examined consisted largely of tuberous vegetable material with seed case fragments and in two cases insects and remains of a (?) gecko.

The material on which the following account is based comprises 23 individuals, belonging to three collections all from the main island, two made personally in November, 1947, and February, 1949, respectively, and a third by a party which included South Australian Museum personnel, in December, 1947. The sex ratio in the combined collection is 16 ♂ ; 7 ♀ . During November and December reproduction was evidently active, all males having enlarged scrotal testes and some females lactating, though no young were taken; in February, however, when only females were taken, their condition was quiescent, with occluded vulvae and strongly retracted nipples.

Ectoparasites were present in large numbers and have been found by H. Womersley to include two species of fleas, *Xenyllopsis cheopis* and *Cerataphyllus fasciatus*; two species of acarids, *Laelaps nuttali* Hirst and *Haemaphysalis leachi* Aud., and the louse *Hoplopleura bidentata*. Of endoparasites an extraordinarily heavy stomach infestation of nematodes was found in several individuals and these have been tentatively identified by Mrs. I. M. Thomas as species of *Physaloptera* and *Protospirura*. About one-third of the specimens examined showed pathological conditions in the tail and manus and pes, with malformation of digits and ulceration of the papillae of facial vibrissae. In spite of these afflictions, however, the rats were commonly vigorous and well nourished, and sometimes fat.

The Greenly Island rat has attained a considerable level of differentiation both from that of the standard series of the Fleurieu Peninsula and from its nearer neighbour *R. greyi murrayi* Thos. of the Pearson Islands, about 60 miles to the nor'west.

It is nearer the latter, especially in the more obvious characters of pelage, but in other important respects is quite distinct and I propose to separate it subspecifically as

RATTUS GREYI PELORI subsp. nov.

It may be diagnosed with respect to *R. g. murrayi*, as follows:

A relatively large form, and when fully adult, thickset and bulky and with powerful hands and feet. General size considerably exceedingly *murrayi* and the tail and pes longer both absolutely and relative to head and body; the pes much modified, broader and with structural differences noted below; tail scales finer; pelage still paler and more grizzled, the ear backs lighter than the head, not darker, and the precarpal bar conspicuous. In the skull the anterior palatal foramina are shorter and the dentition less reduced.

The longest mysticial vibrissa in 13 apparently undamaged examples gave a range and approximate mean of 38-58 (45). The ear is thick in substance and relatively broad with a B/L ratio of ·63-·75 (·69). The manus is stouter than in the Fleurieu series, the B/L ratio averaging ·42 as against ·37, and though the size sequence of the pads is the same, the individual pads are stouter and more squat and the metacarpals nearly always subequal. The pes is also notably large and broad, the breadth ranging from 7-8·5 and the B/L value from ·22-·27 (·25) as against ·21-·24 (·22). The pad sequence is much the same, but the inner metatarsal tends to be smaller and narrower, while the rest of the pads, especially the interdigitals 1 and 4 are rounder. Fresh or alcoholic specimens of *R. g. murrayi* suitable for accurate measurement have not been available, but direct comparison of dried material of all three forms has shown that the agreement of *murrayi* in manus and pes is with the standard Fleurieu series rather than with that of Greenly Island and the above metrical comparison of the two latter is inserted to give an approximate estimate of the difference. The tail is stout and, by mainland standards, short although less so than in *murrayi*, the mean percentage of head and body length being 88 per cent. as against 77 per cent. in the latter; the scale rows are constantly 15 per cm. mid-dorsally in adults, rising to 17 in subadults, as against 12-13 in adults of *murrayi*.

The pelage is subject to much heavier wear than has been observed on the mainland and, as a consequence, differences due to this factor are correspondingly high. The November and December batches contain many thin and lax coats, largely denuded of guards on the rump and with a short replacement coat showing basally here and there on the dorsum. In February, however, the pelage was prime and in point of density about equal to that of the Fleurieu series dorsally, but always thinner ventrally. In spite of these differences, the general colour range is less than in the latter. The following notes are based chiefly on the prime pelage. Middorsally the three piles average 16, 18 and 20 mm. in length, respectively, with guards on the posterior back from 40-45 mm. The subterminal band is a weak yellowish buff, never brown nor rufous, and is longer with less black or brown annulation and less overlay from the guards. The general dorsal colour is a somewhat olivaceous[1] grey brown, near Ridgway's drab, very uniform from the crown of the head to tail base in good pelage but irregularly mottled with wear, and with a tendency in November skins to a warmer scapular and darker lumbar area. The ear backs are paler than the head in dried skins though not always appearing so in life. The sides are cold drab merging imperceptibly with the ventrum which is pale plumbeous basally for three-quarters of its length and weakly tipped with ivory buff, the general effect near drab grey. Manus and pes may be pure white or feebly grizzled with drab or brown and there is always a conspicuous dark precarpal bar on the outer aspect of the forelimb. The tail is long-haired as in *murrayi* with hairs 3-3·5 scales in length when not abraded, and rather erect; its colour

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[1] A skin in the South Australian Museum made up from alcohol after 12 years immersion, shows marked changes from the fresh condition here described.

variable but most frequently a pale drab on all surfaces and with no dorso-ventral contrast.

In pelage *R. g. pelori* shows the same divergent trends from *R. g. greyi* as *R. g. murrayi* does, but carries them a stage further resulting in increased pallor, weaker and yellower subterminal colour and more conspicuous dorsal grizzling, especially on the head where the ear backs are lighter, not darker. In the five skins of *murrayi* which have been used in the comparison the tail is much darker on all surfaces than in the new form but the standard series has shown this character to be so unstable that I hesitate to advance it as a good distinction.

Flesh Dimensions—The following figures give in turn the range and approximate mean for five adult ♂ and five adult ♀, and of the type ♂. Head and body, 158-168 (162·8), 147-162 (154·0), 168; tail, 127-145 (135·7), 137-142 (139·7), 142; pes, 31-32 (31·3), 30·5-31·5 (31·0), 31·5; ear length, 20-20·5 (20·2), 19·5-20 (19·9), 20·5; ear breadth, 13-15 (14·0), 13-14 (13·5), 13; weight in grammes, 110-111 (110·5), 94-105 (98·8), 110.

The adult skull is slightly larger than that of *R. g. murrayi*, but otherwise is in general agreement with it and in particular shares (in varying degree) the three main distinctions of the latter from *R. g. greyi* as defined (*supra*), i.e., slightly greater rostral length, slightly broader bulla, and decidedly reduced molar rows. It differs from *murrayi* in a wider interorbital region, shorter anterior palatal foramina and in a smaller degree of molar reduction, especially noticeable in transverse diameters, which are scarcely below the Fleurieu standards. Other minor differences from *R. greyi greyi* of an average kind are shown in the interparietal which in adults are smaller; in the zygomatic plate which tends to be higher and with a slightly different curvature of the free margin and in the posterior margin of the palate which is evenly rounded and not produced into a spur or prominence at the palation.

Skull dimensions—The following figures give, in turn, the range and approximate mean for five adult ♂, three adult ♀, and the type ♂: Greatest length, 36·6-39·0 (37·6), 36·0-37·3 (36·6), 37·5; basal length, 32·1-35·6 (33·7), 32·0-33·0 (32·4), 34·0; zygomatic breadth, 18·5-19·6 (18·9), 18·4-18·5 (18·47), 19·0; interorbital breadth, 5·5-5·6 (5·56), 5·5-5·8 (5·57), 5·5; nasals length, 14·2-14·8 (14·5), 13·7-14·5 (14·1), 14·8; nasals greatest breadth, 3·7-4·0 (3·8), 3·6-3·7 (3·67), 3·7; palatal length, 18·6-20·7 (19·6), 19·0-19·8 (19·3), 20·1; anterior palatal foramina, length, 6·8-7·2 (7·0), 6·7-6·7 (6·7), 7·1; anterior palatal foramina, breadth, 2·3-2·6 (2·4), 2·2-2·5 (2·3), 2·5; bulla length, 6·2-6·6 (6·4), 6·1-6·2 (6·17), 6·4; $Ms.^{1-3}$, 5·6-5·9 (5·8), 5·5-5·8 (5·7), 5·9.

Type—Adult male; South Australian Museum, registered number M.6268; a field-made skin and prepared skull collected by the writer in November, 1947, on the north slope of the main mass of Greenly Island, at approximately 34°39′S. lat. and 134°49′E. longt.

(e) NORTH GAMBIER ISLAND

This islet of a few hundred acres, and about 150 feet high, lies about a mile and one-half north of the much larger Wedge Island in the Gambier Group at the mouth of Spencer Gulf at 35°08′S. lat. and 136°28′E. longt. approximately.

It is believed to be waterless and has never had human occupation, but long ago—possibly as early as 1820—goats were introduced and have persisted to the present time, and provide an attraction for fishing cutters in search of fresh meat. Originally, the central portions of the plateau were well grassed with *Danthonia* and supported groves of well-grown *Casuarina* trees, but as

a result of an erosion cycle which I have sketched elsewhere (1951), this area has now been denuded to the limestone and only a narrow belt of bush vegetation remains surrounding it on the cliff tops. This vegetated zone is colonized by mutton birds (*Puffinus* sp.) which burrow and by a local form of *Rattus greyi*, which lives chiefly under the tangle of a sprawling bush, *Nitraria schoberi*. The rat was formerly in very large numbers, and boat crews killed them in sport by lifting up the tangle and sending terriers in after them. Although now much reduced, it still seems to have a good hold on these parts of the island, but in a short daylight visit in February, 1949, I succeeded in trapping only three among the limestone blocks of the cliffs on the south-east coast.

These were two males and one female; one of the males with enlarged scrotal testes, the other retracted and the female apparently reproductively quiescent. A motile ectoparasite (? *Hoplopleura*) was noted, but not collected.

Externally, this rat is somewhat intermediate between that of Greenly and Pearson Isles. It is slightly smaller than the former and has a slightly longer and narrower ear, though still broad by mainland standards. The pes, although smaller, is of the same broad robust type, with similarly rounded though smaller pads. Mysticial vibrissae range from 47-55 (50); the tail scales are coarser, 13-14 per cm., and the tail hairs shorter, 2-2·5 scales length. The tone of the dorsal pelage is slightly warmer, but the general condition very similar; manus and pes pure white as they are in a proportion of the Greenly rat.

Flesh Dimensions of the two ♂, and one ♀ are as follows: Head and body, 153-153, 132; tail, 123-136, 130; pes, 29-29, 27; ear length, 21-21, 21; ear breadth, 13-13, 14; weight in grammes, 100-105, 80.

The skull if regarded as fully adult, as the molar wear and zygomatic shape suggest, is the smallest examined in this work and as compared with that of Greenly Island is weak, and fragile and lightly ossified. The nasals and rostrum are shorter and weaker, the bullae smaller, and the anterior palatal foramina slightly longer, but the molars are within the range and therefore comparatively large, in so small a skull.

Skull dimensions of the two ♂ and one ♀ are respectively; Greatest length, 35·0-35·2, 35·2; basal length, 30·0-31·0, 31·4; zygomatic breadth, 17·3-17·7, 18·0; interorbital breadth, 5·1-5·3, 5·2; nasals length, 12·9-13·2, 13·0; nasals breadth, 3·5-3·8, 3·5; palatal length, 17·9-18·6, 18·5; anterior palatal foramina, length, 7·2-7·2, 7·4; bulla, length, —, 6·0, 5·9; Ms.$^{1-3}$, 5·7-5·8, 5·7.

If the characters of the Gambier Island population are reliably represented by these three specimens, it would appear to differ appreciably from that of both Greenly and Pearson islands and, while nearer these, shows some links with the mainland phase from the Gawler River, but with a marked reduction in skull size. The clearances in characters, however, are so small that I have not felt justified in basing another name upon so little material, and defer a decision on its status until an adequate series can be assembled.

Evidence of varying value from miscellaneous sources indicates that "native" rats, presumably of the *R. greyi* type, exist or formerly occurred on several other islands off the South Australian coast, besides those already listed, including the main island of the North Neptune group, Hopkin's, Taylor's, Eyre's, Goat, St. Francis and St. Peter's.

(d) SOUTH-WESTERN VICTORIA

Brazenor (1936) reported on a large series of *R. greyi* from the Portland district, which he compared with both "South Australian" *R. greyi* and with Victorian *assimilis*, and separated subspecifically from the former. Although I agree with his chief findings the first of his comparisons was hampered by

shortage of material and some emendation and amplification of both are called for. The following notes are based upon a batch of twelve taken at Heathmere in December, 1937, and on the east bank of the Glenelg River about 20 miles north-west of that place, in June, 1951. These localities are only 10-20 miles north of Portland in a similar environment and the material is regarded as topotypical of *R. g. peccatus*.

In habits this form differs from *R. greyi greyi* of the Fleurieu Peninsula in being a more consistent burrower; this was confirmed both at Heathmere and on the Glenelg where it was quite numerous, but I doubt whether burrows were plentiful enough to shelter the whole population, part of which probably makes use of surface camps. In December at Heathmere all adult males taken showed enlarged and scrotal testes and females were pregnant.

The range in dimensions shows a plus overlap in the chief items with means averaging about 8 per cent. higher than in the standard series of *R. greyi greyi*. In relation to head and body, the tail and, to a lesser extent, the pes, are longer in the female than in that form, but this change is not shared by the male. Ignoring the sexual difference, it would appear that the chief distinction in the dimensions of the Victorian animal is in an increase of overall size and in a somewhat narrower ear. Brazenor's means of 20 selected specimens are decidedly below mine in ear and pes (and skull length also, see *infra*) and his sample probably includes what is here regarded as a definitely subadult element. I am unable to substantiate his finding that the female is necessarily smaller in linear dimensions than the male, when fully adult as judged by skull characters, nor is this the case with the standard series of *R. g. greyi*, and its use as a differential character against *assimilis* is, I think, invalid. The other metrical proposition which he uses differentially, i.e., that in large specimens of *greyi* the tail is relatively shorter than in small, I am unable to test adequately with *peccatus* or *assimilis*, but it seems to work out in the standard series where (ignoring sex) the six largest give a per cent. tail length of 84-110 (91·6) as against 93-110 (100·7) for the six smallest.

The manus and pes are very similar to those of *R. g. greyi*, the former perhaps a little heavier, but the pes, unlike that of *assimilis*, even narrower. The pads are of the same type, with distinctly angular lateral interdigitals. The mysticial vibrissae range from 47-50 (49) and the tail scales are slightly coarser, with 11-13 (12·6) per cm. middorsally. The mammary pattern, discussed by Tate (1951, 330) in connection with this subspecies, is not characteristic of it, but occurs (with variants) in *R. g. greyi* as well. (*Supra*.)

In the pelage characters of the body, the West Victorian series can be completely merged in that of the Fleurieu Peninsula; it does not yield any examples of the rich coppery variants of the latter, but all its other phases can be closely matched therein, and it offers nothing novel in tone, grizzling or pattern; it is certainly not darker as a whole. On the dorsum of manus and pes the hairs are always decidedly darkened at base and this leads to occasional grizzling, particularly when the covering is sparse, and there are two cases of all dark hairs at base of the claws not noted in other groups. The precarpal bar is usually fainter and sometimes lost, but on the inner aspect of the lower surface of the carpus there is frequently a tract of adpressed, contrasted brown hairs outlining the bases of the metacarpal pads, absent, or very feebly indicated, in the Fleurieu series. The tail is usually appreciably darker above than below, as in the latter, but there are equally striking variations both in its colour and in the prominence of the scale rings. In worn pelage where replacement has begun, there is a tendency for a darker lumbar patch to be isolated as in the November skins from Greenly Island.

Flesh Dimensions—The following figures give in turn the range and approximate mean for the dimensions of three ♂ and four ♀, adult. Head and body, 152-169 (160·0), 153-166 (156·0); tail, 138-155 (149·0), 140-163 (154·7); pes, 31·5-33·5 (32·5), 30-32·5 (31·6); ear, length, 22-23 (22·5), 21-23 (22·5); ear, breadth, 13·6-13·8 (13·7), 13·8-15·0 (14·4); weight in grammes 100-130 (115·0), 85-130 (110·0).

The adult skull is larger than in *R. greyi greyi*, with the female giving higher values in most measurements than males. The range in the majority of items shows a plus overlap with that of the standards with an average increase in the means of the order of 5 per cent. in most longitudinal dimensions. It is relatively narrower zygomatically, with slightly longer rostrum and relatively shorter tooth rows with broader molars. A notable nonmetrical distinction from the primary form is to be found in the temporal crests, which are more strongly developed and produced anteriorly on to the supraorbital margins which in consequence are distinctly ridged.

Skull Dimensions— The range and approximate mean follow in turn for four adult ♂, three adult ♀, and a single anomalous stunted adult or aged ♀, which gives values below the minima for the Fleurieu series, and which cannot be regarded as a normal intergrade between *R. g. greyi* and *peccatus*:—Greatest length, 36·9-38·5 (37·5), 37·7-38·8 (38·2), 34·0; basal length, 32·8-35·0 (33·8), 33·6-34·3 (33·9), 29·8; zygomatic breadth, 18·3-18·9 (18·5), 18·3-18·7 (18·5), 17·3; interorbital breadth, 5·3-5·5 (5·4), 5·3-5·5 (5·4), 5·1; nasals length, 14·2-15·6 (14·8), 15·0-15·2 (15·1), 13·0; nasals greatest breadth, 3·7-4·0 (3·9), 3·6-3·8 (3·7), 3·6; palatal length, 19·6-21·5 (20·2), 20·3-20·6 (20·4), 18·1; anterior palatal foramina, length, 7·3-8·0 (7·6), 7·9-8·0 (7·95), 6·8; anterior palatal foramina, breadth, 2·5-2·8 (2·6), 2·5-2·5 (2·5), 2·5; bulla, length, 6·5-6·6 (6·55), 6·5-6·8 (6·6), 5·9; Ms.$^{1-3}$, 5·9-6·4 (6·1), 6·0-6·4 (6·2), 5·5.

Rattus greyi peccatus is undoubtedly a valid form, recognisable beyond the limits of the conventional 75 per cent. allocation, by metrical, pelage and cranial characters. It is at present known from a very restricted area of south-western Victoria at sea level, in ecological conditions appreciably different from those of the South Australian highlands, which harbour the primary subspecies. To what extent it interdiffuses with *assimilis* to the east and how effective the Glenelg River is as a barrier to its westerly drift, are matters which await further field work.

4. *RATTUS ASSIMILIS* GOULD

The relationships of this species to *R. greyi peccatus*, to which it bears much external resemblance, have been examined by Brazenor (1936) in broad outline with a large series of Victorian specimens. There is need, however, for a more detailed statement of its characters and range of variation before these can be regarded as well established. The material in hand is inadequate for this, but for the purpose of a limited and provisional check, skins and skulls of some 15 individuals are available. These belong to two batches personally taken in January, 1928, on upper Ryan's Creek in the Tolmie district of northeast Victoria, and in December, 1928, at Hillas Brook in the Batlow district of southern New South Wales. Both localities are highland sites, the second above 3,000 feet. In addition, I have examined miscellaneous specimens from French Island in Westernport Bay, Victoria, and from Dorrigo and the Barrington Tops in New South Wales. At the Ryan's Creek camp the species was plen-

tiful though not at all obtrusive and was first taken unintentionally in wallaby and opossum snares under tree ferns in a wet gully and later was trapped with bread baits in the undergrowth of dense wattle scrubs. At Hillas Brook it was taken in the same way under bracken in more open valleys of big eucalypts, and a few also in a barn where they had begun to raid potatoes in sacks — a type of depredation which *R. greyi* in South Australia never seems to attempt. Whether this combined series is as homogeneous subspecifically as current nomenclature would imply, may be questioned but it suffices for a general appraisal of the *R. g. peccatus-assimilis* relation.

Dimensions of adults just overlap the maxima for those of *peccatus*, as quoted above, in head and body, pes and ear, but the means are higher, decidedly so (10-12 per cent.) in the case of the first. The means for tail length are equal in the case of the males and lower with the single female. Proportionally to head and body, therefore, the pes and ear are slightly shorter than in *peccatus*, and the tail markedly so, with a mean for the two sexes of 83 per cent. as against 95 per cent. in the latter; this finding is supported by the short-tailed condition of the cotypes (80-84 per cent.), but conflicts with Brazenor's 101 per cent. as a mean for 20 *assimilis*. No weights are available, but would probably be much higher than for any form of *R. greyi*.

In dried specimens both manus and pes appear to be much stouter than in *R. g. peccatus*, though the pads are of the same general type. Brazenor, however (*op. cit.* Pl. XIII, 2 d) figures a somewhat more elongated inner metatarsal. In the manus the digital rings are increased to 6 and, in the pes, to 8, and they are less divided than in the forms of *R. greyi*. Mystical vibrissae in five undamaged adults range from 59-67 (61), which is much longer than in *peccatus* and the tail scales are slightly coarser, 11-12 (11·7) per cm.

In pelage characters the group shows an extraordinary range of variation, due partly to phase, but partly to local or individual influences, and it is obvious that until comprehensive series are examined illustrating the entire sequence of the coat replacement, only tentative conclusions are possible under this head. Brazenor (1936, 67) has already stated that the pelage of *assimilis* is indistinguishable from that of *R. greyi peccatus* of the Portland district. So far as the Victorian specimens of the present series are concerned, this is substantially true. The single French Island skin is much richer coloured and more cupreous in tone than any of my *peccatus*, though it can be matched in the Fleurieu Peninsula, and of the remainder it is generally true that the coat is somewhat more spinous dorsally, the darkening of manus and pes more frequent, and the presence of the brown infracarpal tract more constant than in the latter. The precarpal bar is present in two skins only. The New South Wales examples from Batlow and Dungog are appreciably distinct being colder in tone and with a finer ticking.

Flesh Dimensions — Four adult males and one adult female give the following values:—Head and body, 168-195 (179), 173; tail, 143-157 (150), 142; pes, 33-35 (33·5), 34; ear length, 22-24 (23·2), 23.

Skull size in these two groups is consistently much larger at all comparable stages of growth than in *R. g. peccatus*. The range in seven of the eleven dimensions studied shows a plus clearance from that of the latter, with the means of the chief longitudinal dimensions 10 per cent. higher, and the overall superiority in size is still more impressive in direct visual comparison. The chief departures from coproportionality with *peccatus* as gauged by the percentage relation to the greatest length of skull, are: Shorter rostrum, shorter and much narrower anterior palatal foramina (− 6 and − 25 per cent. respectively), shorter bulla (− 10 per cent.), and longer molar rows (+ 14 per cent.).

In nonmetrical cranial characters there is considerable variation and overlap, but the following may be noted as valid differential trends. In the nasals there is a distal shift in the maximum width which leads to a straight, more wedge-shaped outline than is usual in any of the forms of *R. greyi*; the temporal and supraorbital ridges are similar in outline but more strongly developed; the dorsal profile is straighter and less arched; and the posterior half of the anterior palatal foramina is more narrowed and parallel-sided than the anterior, with a characteristic change of shape.

One skull presents the anomaly of a paired interparietal (Pl. 1, Fig. G).

Skull Dimensions — The values for seven adult males are as follows:—Greatest length 40·0-43·1 (41·4); basal length, 35·3-39·1 (36·9); zygomatic breadth, 20·0-21·4 (20·8); interorbital breadth, 5·7-6·0 (5·9); nasals lengths, 15·0-17·0 (15·7); nasals greatest breadth, 4·1-4·5 (4·3); palatal length, 21·6-23·5 (22·5); anterior palatal foramina, length, 7·5-8·3 (7·9); anterior palatal foramina, breadth, 2·0-2·5 (2·3); bullae, length, 6·2-6·7 (6·5); Ms.$^{1-3}$, 7·0-7·6 (7·3).
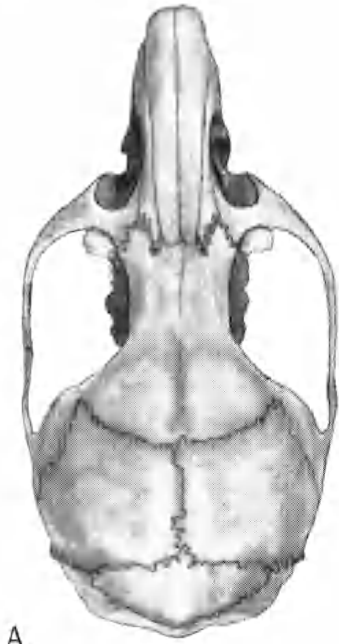
5. INTERRELATION OF *R. ASSIMILIS*, *R. GREYI* AND *R. FUSCIPES* WATERHOUSE

Ellerman (1949) considered *R. assimilis* and *R. greyi* to be conspecific, a view with which Tate (1951) evidently sympathised, though he did not give effect to it in nomenclature. Though they are undoubtedly very closely related animals, a study of the two forms, which may be assumed to be in contact in mid-Western Victoria, has convinced me that the differences separating them are more than subspecific and confirms me in the opposite and older view. Although occasional specimens may transgress the limits of the three groups, a more or less clinal relation in general body size subsists between the east to west series, *R. assimilis* (?assimilis), *R. greyi peccatus*, and *R. greyi greyi*, with a much steeper gap between the first two forms, but this trend is not continued into the offshore colonies of Eyre Peninsula where, in the case of *R. g. pelori* at least, a slight secondary enlargement has taken place.
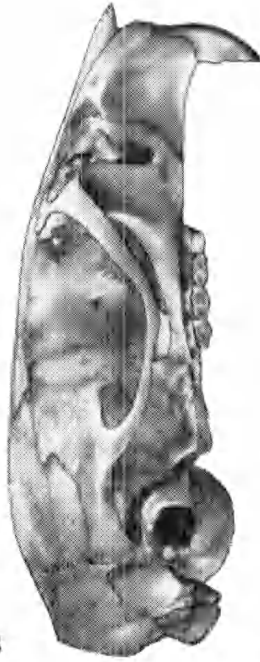
These island forms, although well differentiated, have so many unmistakable links with the Fleurieu Peninsula population that their relegation to *R. greyi* seems the only natural course. The alternative allocation to *R. fuscipes*, which is regarded as having a modified representative on Mondrain Island on the continental shelf of Western Australia, has some attractions on palaeogeographic grounds and is foreshadowed in the views of Ellerman (*op. cit.*). I have not tested this *de novo*, but if the generally accepted links of *R. fuscipes* with *R. lutreola* are well founded (and they have been recently reaffirmed by Tate (1951) with good material), it would seem to be strongly contraindicated. None of the forms here considered show any convergence cranially to *R. lutreola* as known in South Australia.
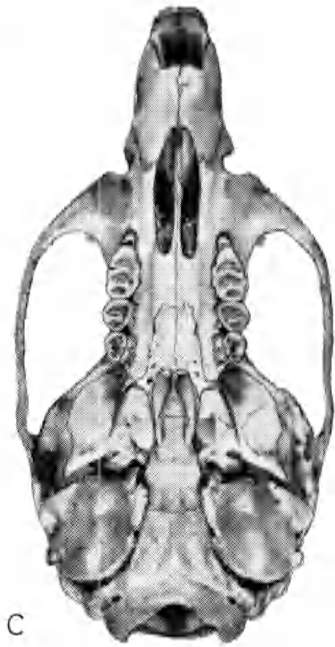
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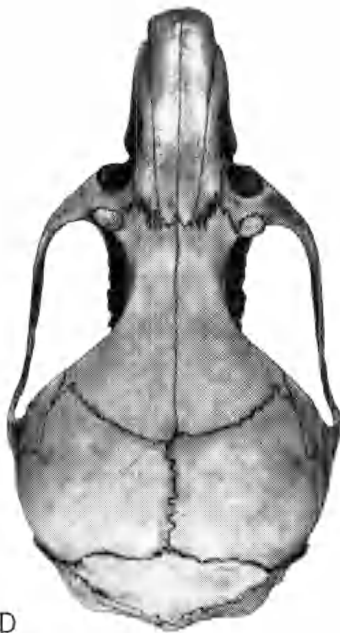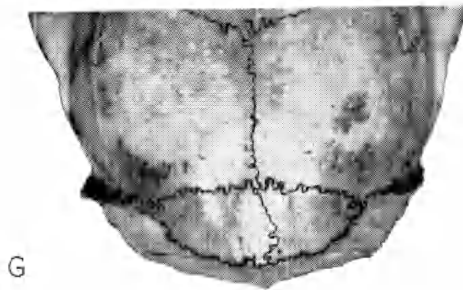GLAUERT, L., 1950. Jour. Roy. Soc. West. Aust., XXXIV, pp. 115-134.

Plate 1

A

B

C

D

E

F

G